COMPUTER-AIDED RESTORATION OF A LATE CAMBRIAN CERATOPYGID TRILOBITE FROM WALES, AND ITS PHYLOGENETIC IMPLICATIONS

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ABSTRACT. Tectonic deformation is liable to affect the diagnostic characters of fossils, but its effects can be removed with the help of a computer-graphic technique, which is here applied to trilobites for the first time. *Dikelocephalus? discoidalis* Salter, 1866, with its putative synonym *D.? celticus* Salter, 1866, is known only from distorted specimens collected from the upper part of the *Parabolina spinulosa* Biozone in the Dolgellau Formation (upper Cambrian) of North Wales. It has been reconstructed by removing tectonic deformation. *D.? discoidalis* is now referred to *Cermatops* Shergold, a member of the Subfamily Iwayaspidinae; this group is considered to be a paraphyletic subgroup within the Family Ceratopygidae.

IN north-west Europe the Late Cambrian faunas are dominated by olenid trilobites, a specialized group that was adapted to oxygen-deficient environments (Henningsmoen 1957), whereas such cratonic realms as North America, Australia, northern China and Siberia, each supported a diverse and partly endemic suite of genera (Palmer 1977). Besides the agnostids, one of the most widely distributed trilobite groups is the Family Ceratopygidae, members of which are known from most areas yielding late Middle Cambrian to Tremadoc faunas, though despite much recent work the full biostratigraphical potential of the group has yet to be realized. *Proceratopyge* is recorded in the English Midlands (Rushton 1983) and *Ceratopyge* itself from the Tremadoc of North Wales but until now no ceratopygids have been recorded from the Merioneth Series in Wales. However, we here refer Salter's *Dikelocephalus*? species from the Merioneth Series of North Wales to the ceratopygid genus *Cermatops* Shergold, 1980. Dikelocephalids are common only in North American Trempealeauan deposits from shallow shelf environments (Taylor 1977). Their supposed presence in black shales from North Wales was remarkable, both on account of the slope setting there and because the European *P. spinulosa* Biozone is correlated with the lower Franconian *Taenicephalus* Biozone of North America, well below the Trempealeauan. The new assignment negates a suggestion by Conway Morris and Rushton (1988, fig. 3) that dikelocephalids migrated from outer-shelf environments onto the North American craton, but fits well with the known biogeography of ceratopygid trilobites.

OCCURRENCE

Salter's '*Dikelocephalus*' material came from the locality 'Ogof-ddû', 1 km east of Criccieth, Gwynedd, North Wales, *D.? discoidalis* being based on cephala and *D.? celticus* and *D.?* sp. on pygidia. Ogof-ddû refers to the cliff-section Rhiw-for-fawr (around National Grid reference SH 5135 3795) that extends from the top of the Ffestiniog Flags Formation, through the whole Dolgellau Formation, to the lower part of the Tremadoc (Fearnsides 1910, p. 153); the section encompasses several trilobite biozones. In 1951 officers of the British Geological Survey (BGS) examined the section bed-by-bed and collected fossils throughout; Stubblefield (1953) reported preliminary results. Review of the BGS collection shows that the lowest 13 m of the Dolgellau Formation is referable to the *Parabolina spinulosa* Biozone. Material of '*Dikelocephalus*' (now *Cermatops*) was collected only from 8·5 to 9·0 m above the base, that is, entirely within the upper part of the *P. spinulosa* Biozone. The *Cermatops* are associated with the following fossils:

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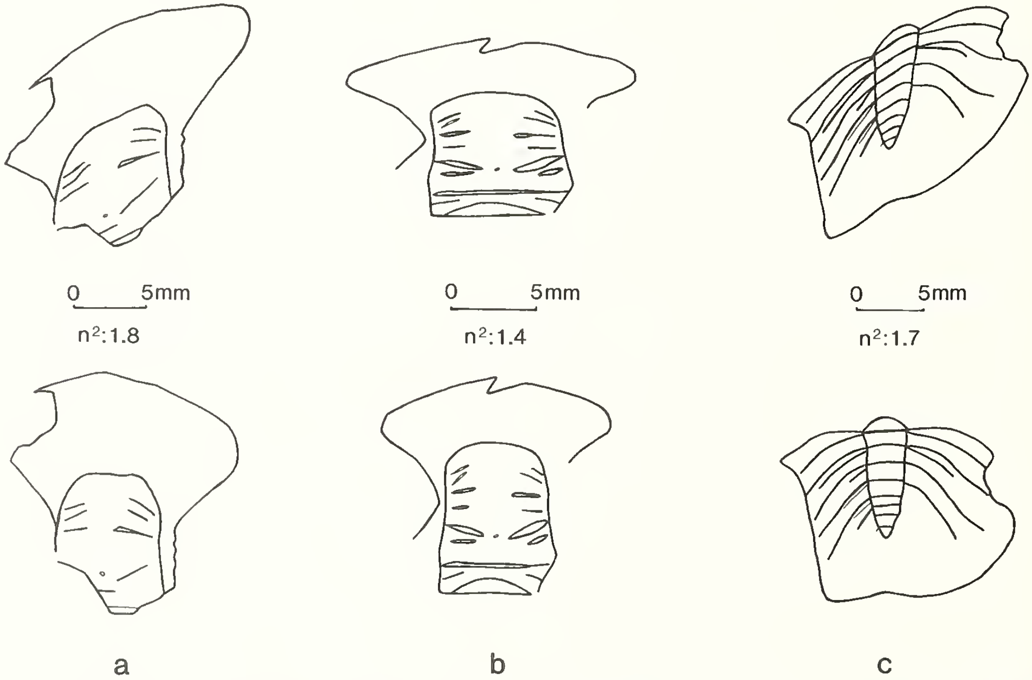
Homagnostus obesus laevis Westergård, *Pseudagnostus cyclopyge* (Tullberg), *Parabolina* cf. *spinulosa* (Wahlenberg), *Parabolinites*? sp., *Lingulella* sp., *Orusia lenticularis* (Wahlenberg) [abundant] and *Stenotheca* sp.

Fearnsides collected a pygidium referable to *Cermatops discoidalis* (Pl. 2, fig. 9) from the stream section below Penmorfa Church (Salter 1866, p. 250).

The only other material known to us was collected by Shackleton (1959, p. 222) from the cliff above Cwm-y-ffynnon (SH 5403 5141), 7·5 km west-south-west from the summit of Snowdon and about 14 km N of Ogof-ddû, where rare *Cermatops* fragments are associated with abundant *O. lenticularis* and *Homagnostus*, *Pseudagnostus*, *Parabolina* aff. *mobergi* Westergård, *Parabolinites*? sp. and *Maladoidella*? *abdita* (Salter). Apart from the abundance of *O. lenticularis* this fauna does not yield clear evidence of the *P. spinulosa* Biozone, but fragments of *P.* aff. *mobergi* are present at the top of the *P. spinulosa* Biozone at Ogof-ddû.

CORRECTION OF DISTORTION

Salter's (1866) *Dikelocephalus*? from the Dolgellau Formation are strongly deformed. To assess the generic position of these forms it was desirable to restore the original shape, and to this end we used a computer-graphic method employed at the British Museum (Natural History). The technique involved the digitization of camera lucida or photographic images of the specimens; the digitized images were then displayed on a monitor and progressively adjusted until bilateral symmetry was achieved (see Jefferies *et al.* 1987 for details). The validity of this method was tested using slabs in which various specimens were preserved in different orientations; some had the sagittal axis parallel to the principal component of strain (x axis of the strain ellipse) whereas in others it was perpendicular or oblique. Bilateral symmetry was restored to each specimen individually and values of n^2 (the proportionate increase of the y co-ordinate relative to the x co-ordinate) compared.



TEXT-FIG. 1. Examples of computer restorations giving bilateral symmetry. Above – *camera lucida* sketches; below – after restoration. n^2 represents the factor required to restore symmetry to each drawing.

Within individual slabs the value of n^2 required for each specimen was identical; this validated the use of bilateral symmetry as a criterion for restoring the shape.

The program gave an approximation to the original shape (see text-fig. 1) but did not produce perfect restorations; in many cases the x–y plane of the strain ellipse was not exactly the same as the dorso-ventral plane of the specimens, and in some cases pyrite crystals caused local inhomogeneities of strain. Several specimens had been cracked during compression and prior to tectonic distortion. These factors did not, however, significantly limit the use of the method in determining a generalized representation of the overall shape, and this proved important for taxonomic assessment.

The bilaterally symmetrical restorations of cranidia and pygidia provided by the computer method were scaled to a standard size using a Rost planvariograph. These images were superimposed and an overall representation of original shape inferred (see text-fig. 2). Because of the complexity of post-mortem deformation, particular weight was given to those specimens which showed least original distortion (for example the pygidium in Pl. 2, fig. 9). The three specimens of free cheeks were not analysed on the computer because two of the specimens were comparatively undistorted and also because their shape could largely be inferred from the cranidial restoration. As the sagittal axis of the single hypostome was parallel to the x axis of strain, it was not possible to restore its shape; the outline of the hypostome in the reconstruction is therefore dotted. In the absence of complete specimens the relative size of cranidium and pygidium was estimated from the size-ranges of the specimens available. Particular features, such as the sculpture and median tubercle, were included in the reconstruction only if they were recognized in at least two specimens.

SYSTEMATIC PALAEONTOLOGY

Superfamily ASAPHACEA Burmeister, 1843
Family CERATOPYGIDAE Linnarsson, 1869
Subfamily IWAYASPIDINAE Kobayashi, 1962
Genus CERMATOPS Shergold, 1980

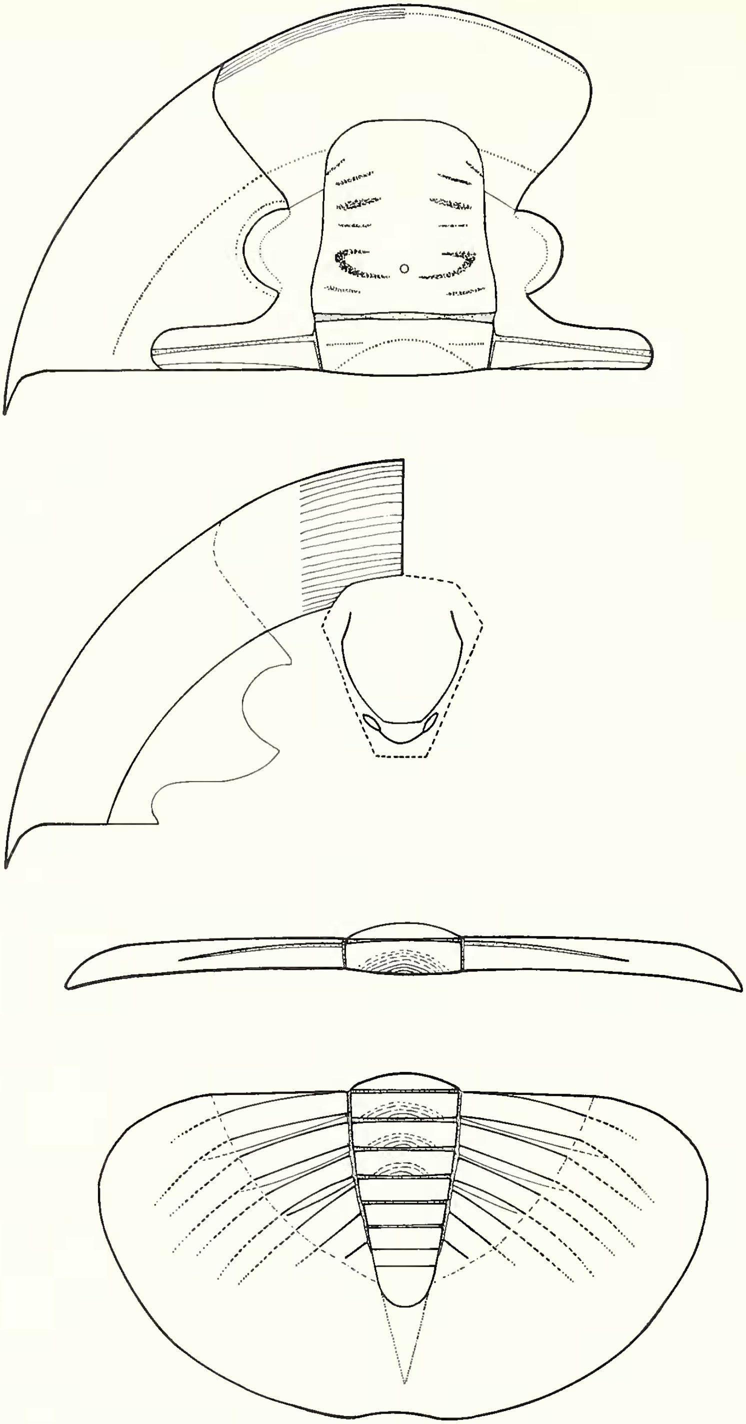
Type species. C. vieta Shergold (1980, p. 87, pl. 34, figs. 3–11). [Names with *-ops* are treated as masculine so the specific name is changed here to *vietus*.]

Diagnosis. Ceratopygid trilobites without macropleural pygidial spines (Subfamily Iwayaspidinae), having a subquadrate glabella showing several pairs of furrows and muscle-scars anterior of S1; palpebral lobe does not reach axial furrow; pygidium transversely semi-oval, the pleural segments having reduced propleural bands. The generic and subfamilial classifications are discussed below.

Cermatops discoidalis (Salter, 1866)

Plates 1 and 2; text-figs. 1, 2, 3*a*, 4

1866 *Dikelocephalus*? (*Centropleura*?) *celticus*, n. sp.; Salter, p. 304, pl. 5, figs. 21 and 22.
1866 *Dikelocephalus*? (*Centropleura*?) *discoidalis*, n. sp.; Salter, p. 304, pl. 5, figs. 18, 18*a*, 19.
1866 *Dikelocephalus*? (*Centropleura*?) sp.; Salter, p. 305, pl. 5, fig. 20.
1868 *Dikelocephalus*? *Celticus* Sal., *D.*? *discoidalis* Sal.; Belt, p. 6 [gives horizon, but incorrectly].
1914 *Dikelocephalus celticus* Salter, *D. discoidalis* Salter; Walcott, pp. 350, 366 [mentioned as generically indeterminate].
1919 *Dikelocephalus discoidalis* Salter; Lake, p. 115, pl. 14, figs. 2–5 only [not figs. 6 and 7, ? = *Lakella invita* (Salter)].
1919 *Dikelocephalus celticus* Salter; Lake, p. 116, pl. 14, figs. 8–10.
1935*a* *Briscoia celticus* (Salter), *B. discoidalis* (Salter); Kobayashi, pp. 51–52 [transferred to *Briscoia*].
1946 *Dikelocephalus celticus* Salter; Lake, p. 343 [discusses similarity to *Briscoia*].
1953 ‘*Dikellocephalus*’ *celticus* Salter; Stubblefield, p. 56 [discusses horizon].
1988 *Briscoia*? *celtica* (Salter, 1866); Morris, p. 38 [listed].
1988 *Briscoia*? *discoidalis* (Salter, 1866); Morris, p. 38 [listed].



TEXT-FIG. 2. Restoration of *Cermatops discoidalis* (Salter), about × 3. Dorsal view of cranidium: the dorsal terrace-ridges are shown on the left side of the preglabellar field, the border furrow is indicated on the right. Ventral view of right free cheek and hypostome; terrace-ridges are shown on a representative area; hypostomal outline inferred (dashed), course of dorsal suture indicated (pecked). Dorsal view of thoracic segment. Dorsal view of pygidium.

Type material. The lectotype of *D.*? *discoidalis*, selected by Morris 1988, p. 38, is BGS GSM 10214 (Pl. 1, fig. 3); it is the original of Salter's fig. 18 and Lake's fig. 2. Paralectotypes include cranidia GSM 10209 (Lake's fig. 3), 10210 (Salter's fig. 19 and Lake's fig. 4) and 10216; and free cheeks GSM 10213, 10213A (Salter's fig. 18*a* and Lake's fig. 5) and 10215. The lectotype of *celticus*, selected by Morris 1988, p. 38, is GSM 10206A (Pl. 2, fig. 3) and 10206 (counterparts), the original of Salter's fig. 22 and of Lake's fig. 9. The paralectotypes include the original of Salter's fig. 21 (GSM 10208), and possibly the unfigured specimens GSM 10212, BGS GSd 4587 and two pygidia collected by Homfray (Sedgwick Museum SM A932). Other material. From Ogof-ddû: GSM 85214 (Wyatt-Edgell Coll.), SM A50349-50354 (Fearnsides Coll.), and about forty specimens and fragments collected by S. W. Hester for the Geological Survey in 1951, numbers prefixed Hr. From Penmorfa, SM A51599 (Fearnsides Coll.). From Cwm-y-ffynnon, five specimens presented to the BGS by Professor R. M. Shackleton.

Description. Glabella widest (tr.) at midlength (sag.) of L1 (= posterior lateral glabellar lobe). Lateral margins subparallel anterior of S1 (posterior lateral glabellar furrow). Glabella with rounded anterolateral corners and straight anterior margin. S1 furrows crescentic, strongly curved, half of glabellar width, shallow adaxially, deeply incised in distal third, not connecting with axial furrow, anterior part weaker than posterior. S2 deepest distally, transverse, crossing one-fifth of glabellar width; S3 oblique inwards and forwards, one-fifth of glabellar width, deepest at mid-length (tr.). L3 short (exsag). Shallow intercalated furrows subparallel to SO across distal quarter of L1. Median tubercle within bifurcation of S1. Shallow furrows intercalated within L2 and anterior of S3. Glabella lacks sculpture. Occipital furrow deepest distally, shallow in axial third. A low ridge arches anteriorly from posterior border of occipital ring, occupying medial four-fifths of occipital width and extending three-quarters of occipital length (sag.). Shallow transverse furrows run adaxially, about one-third of occipital width (tr.). Axial furrow shallow in front of glabella.

Preglabellar field broad, over half as long as pre-occipital glabella, and over twice as wide as occipital ring. Border low, short (sag.), anterior margin slightly angular axially. Terrace-ridges on border face anteriorly. Anterior border furrow crescentic, weakly defined. Preocular sutures diverge forwards at 45 degrees to the sagittal line, then curve in and extend along anterior margin of cephalon. Paradoublural line runs obliquely backwards from anterolateral corner of glabella, subparallel to weak eye ridge. Fixigena narrowest (tr.) opposite L3. Palpebral lobe arcuate, one quarter the length of cranidium, widest (tr.) opposite L2. Palpebral area slopes steeply into axial furrow. Palpebral furrow weakly developed. Posterolateral border area wider (tr.) than occipital ring, straight, narrow (exsag). Postocular suture transverse, subparallel to posterolateral margin. Posterior marginal furrow deeply incised. A shallow furrow runs outwards parallel to posterior margin for four-fifths of width of posterolateral border. Estimated length of cephalic axis in various specimens is 5–15 mm.

Free cheeks arcuate, border smooth. Genal spine short, its base much narrower (tr.) than width of doublure. Median suture present. Portion of ocular platform within paradoublural line one-fifth of fixigenal medial width (tr.), bounded adaxially by upraised flange. Adaxial margin of doublure sub-parallel to cephalic margin; a slight flexure in its anterior portion presumably accommodated the anterior edge of the hypostome. Doublure extends about three-quarters of the distance from margin to ocular incisure. About twenty terrace-ridges present on doublure, continuous, gently sinuous, steeper slopes facing abaxially, most closely spaced at inner and outer margins.

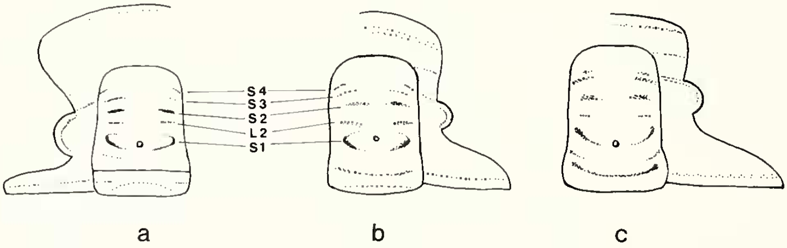
Associated hypostome elongate. Anterior border and anterolateral wing not preserved. Lateral border narrow (tr.) dipping steeply into border furrow; posterior border flatter, longer (sag.) than wide. Median body ovoid. Anterior lobe inflated, posterior lobe gently convex. Median furrow complete, connecting with border furrow. Maculae prominent, ovoid. Sculpture not observed.

Number of thoracic segments unknown. Associated thoracic segment shows articulating furrow deeply incised distally, more shallowly in medial third. An arcuate set of fairly continuous terrace-ridges covers the posterior part of the axial ring. Axial furrows parallel to sagittal axis. Pleura gently curved posteriorly. Pleural furrows deeply incised.

Pygidium sub-elliptical, wider than long. Margin entire, with slight post-axial emargination developed in larger specimens. Axis narrow, convex, tapering evenly posteriorly, about three-quarters of pygidial length and about one quarter of maximum pygidial width. Articulating half ring short (sag.), crescentic. Axis generally of six rings and terminal piece, a poorly defined seventh ring present in some specimens. A set of arcuate posteriorly facing terrace-ridges, similar to those on the thoracic segment, run from posterior border of axial rings. Ring furrows deeply incised distally, shallow adaxially. Axial furrow deeply incised. Post-axial ridge narrow (tr.) where present, extends to posterior margin. Interpleural furrows narrow, firmly incised, extending almost to pygidial margin. Pleural furrows broad, shallow. Five to seven pleurae present, sixth and seventh poorly defined. First pleura contains equally divided pro- and opisthopleurae; pleural and interpleural furrows geniculate at paradoublural line. Subsequent pleura show relative reduction of length and width of propleura. Propleura absent from fifth (and subsequent) pleura, where pleural furrows are undifferentiated from interpleural furrows. Terrace-ridges weakly developed on propleurae. Doublure wide, extending inwards to posterior end of axis, and inwards from anterolateral pygidial margin for half pleural width (tr.). Terrace-ridges of doublure have high relief, steeper slopes facing outwards, distributed most densely along adaxial portion. Estimated length of various pygidia is 5–25 mm.

Interpretative remarks

1. Lateral glabellar furrows. The glabellar furrows of *C. discoidalis* are difficult to interpret because they are variously altered and masked by tectonic compression. Lake thought that the S1 furrow was transcurrent, as in other *Dikelocephalus*. Such a feature is seen only in the most compressed cranidium (Pl. 1, fig. 6), and is contradicted by other specimens and our reconstruction. Salter correctly described the obliquity of the furrows – S1 sloping inwards and backwards, S2 transverse, S3 inwards and forwards – though neither his figures nor Lake's show this clearly. Our interpretation (text-fig. 3) is based especially on the lectotype (Pl. 1, fig. 3) and on the new material (e.g. Pl. 1, fig. 4). The strongest furrow, with inner ends opposite the glabellar tubercle, is interpreted as S1, as is typical of the Ceratopygidae. The comparatively well-marked furrows opposite the anterior half of the palpebral lobes are homologized with S2 of the primitive asaphine pattern (Fortey and Chatterton 1988). The furrow interpreted as S3 is weaker and lies anterior to the front of the palpebral lobe; it is seen in several specimens but is obscured by a misleading crease in GSM 10209 (Pl. 1, fig. 1). A short furrow close to the axial furrow and just in front of S3 is referred to as S4 – a similar furrow is seen in *Guozia crassa* (text-fig. 5*h*). Some specimens show weak transverse furrows on glabellar lobes L1 and L2. Those on L1 are present in some iwayaspidines, as remarked



TEXT-FIG. 3. Suggested interpretation of glabellar furrows in *a Cermatops discoidalis* and *b C. vietus*. *c* is *C.*? *tenacella*, based on Xiang and Zhang 1985, pl. 41, fig. 11.

EXPLANATION OF PLATE 1

Figs. 1–9. *Cermatops discoidalis* (Salter, 1866), all from the *Parabolina spinulosa* Biozone of Ogof-ddû, west of Criccieth, North Wales (National Grid ref. SH 5157 3787 approx.). All these specimens are in the collections of the Biostratigraphy Research Group of the British Geological Survey (BGS), Keyworth, Nottingham. All were whitened before photography and, unless otherwise indicated, are internal moulds. 1–6, 9, cranidia. 1, GSM 10209, ×3; an *Orusia lenticularis* lies to the right of the glabella. 2, Hr 927A, ×3. 3, Lectotype, GSM 10214, ×3. 4 and 5, Hr 948, showing glabellar furrows, and latex cast of counterpart Hr 948A, showing palpebral lobes. Both ×4. 6, GSM 10210, ×4. 7 and 8, free cheeks; 7, GSM 10213, showing the doublure forward of preocular suture and behind it a pyrite infilling between the doublure and the dorsal surface. 8, latex cast of Hr 937, showing small genal spine (slightly retouched). 9, Hr 927B, ×3·2. On the same block as Fig. 2, but oriented at right angles to it. The originals of Figs. 3, 6, 7 were illustrated by Salter 1866, pl. 5, figs. 18, 19, 18*a*; those of Figs. 1, 3, 6, 7 were illustrated by Lake 1919, pl. 14, figs. 3, 2, 4, 5 respectively.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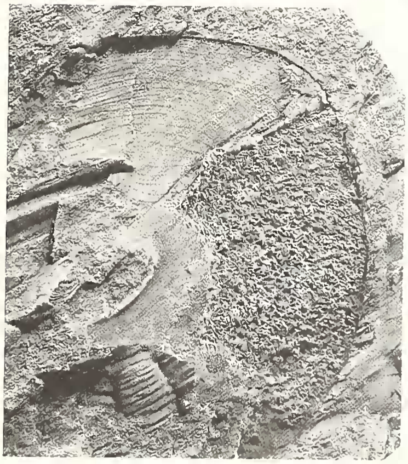
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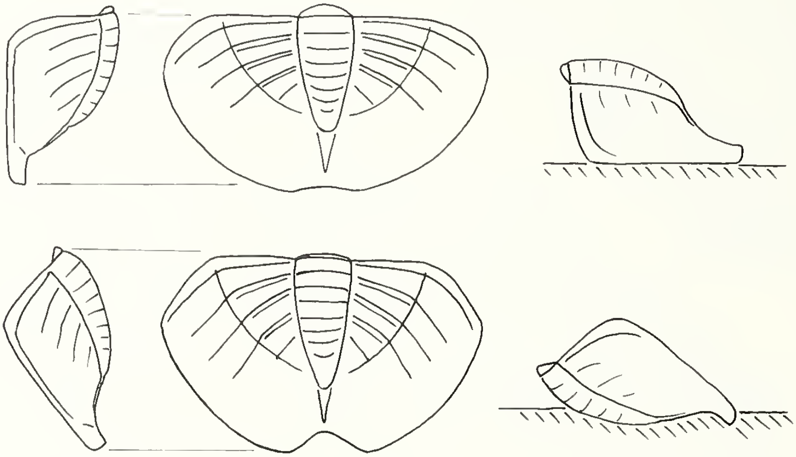
HUGHES and RUSHTON, *Cermatops discoidalis* below, and in some olenids (Rushton 1982). The L2 furrows are weak in *C. discoidalis* but there is a pair of stronger impressions in a similar position in *C. vietus* (Shergold 1980, pl. 34, figs. 3 and 6).

2. Association of the pygidium. Salter assigned the cephalon and pygidium to different species for reasons of caution. Their association in the newer material and their congruence with other Iwayaspidinae indicates that Lake was right to suppose that they belonged to one species.

3. Pygidial shape. The pygidia that Salter described as *D.*? *celticus* differ from those of *D.*? sp. because the length/width ratio is greater, the posterior margin is indented and the pleural furrows are more swept back. Lake thought that these were the same species differently compressed; we believe that he was correct. The differences are readily understood if the pygidium was considerably convex and the posterior margin was arched upwards rather than indented. Viewed from above the pygidium is relatively short, the anterior margin straight, the pleurae direct and the posterior arch nearly invisible (text-fig. 4). This is the '*D.*? sp.' configuration. Viewed obliquely from above and behind, however, the projected length is greater, the anterior margin and pleurae sweep backwards and the posterior arch is more visible (text-fig. 4) – the '*celticus*' configuration. One reason why the pygidium should appear in two forms is that moulted pygidia could come to rest either on the doublure or upside-down on the dorsal surface; flattening by compaction would then give projections corresponding to the two appearances described above.



TEXT-FIG. 4. Sketches to illustrate the differing appearances of the pygidia of *Cermatops discoidalis* according to whether they were deposited dorsal side up (above) or inverted (below).

EXPLANATION OF PLATE 2

Cermatops discoidalis (Salter, 1866). All are from Ogof-ddû, west of Criccieth, North Wales (National Grid ref. SH 5157 3787), except for Fig. 9 which is from Penmorfa Church 2 km west of Tremadog, North Wales (about SH 5418 4030). Figs. 5, 7 and 9 are in the Sedgwick Museum, Cambridge (SM); all the other specimens are in the collections of the Biostratigraphy Research Group of the British Geological Survey. All were whitened before photography and, unless otherwise indicated, are internal moulds. 1–5, 7, 9, 10, pygidia; 6, hypostome; 8, thoracic segment. 1, Hr 925 (external mould), ×3. 2, GSM 10212, ×3. 3, GSM 10206A, ×3. 4, GSM 10211, ×4. 5, two pygidia showing terrace-lines on the doublure; SM A.50349, ×3. 6, fragmentary hypostome, Hr 923, ×6. 7, SM A.933, ×4. 8, thoracic segment, GSM 10216, ×2. 9, least distorted pygidium, SM A.51599, from Penmorfa, ×4. 10, latex cast of GSM 10208, ×2. The originals of Figs. 3, 4, 10 were illustrated by Salter 1866, pl. 5, figs. 22, 20, 21, and by Lake 1919, pl. 14, figs. 9, 10, 8 respectively.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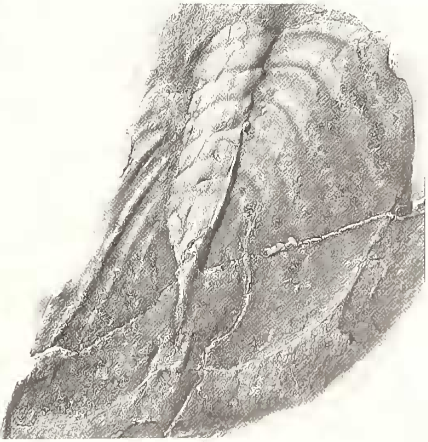
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HUGHES and RUSHTON, *Cermatops discoidalis*

Specific differentiation. The cephalon of *C. discoidalis* differs most obviously from *C. vietus* in having larger eyes, a longer and wider frontal area with more divergent preocular sutures and a smaller genal spine. The same cranidial features distinguish it from *C.? tenacella* (Xiang and Zhang 1985, pl. 41, fig. 11). The pygidium of *C. discoidalis* differs from those of *C. vietus* and *C.* sp. of Shergold (1980, pls. 34 and 35) because it has several clearly defined axial rings (six or more rather than three or four). *C. discoidalis* also has a slight posterior indentation in the pygidium.

Generic position. Shergold referred only *C. vietus* and some unnamed pygidia to *Cermatops*. *C. discoidalis*, as reconstructed here, shows many similarities with *C. vietus* and these we consider to outweigh the obvious differences.

Glabellar structure. In ceratopygids S1 has an unusual crescentic or longitudinal form, and most iwayaspidines show this and a conventional S2 and S3. Both *C. vietus* and *C. discoidalis*, unlike other iwayaspidines, show four pairs of furrows anterior of S1, though their homologies with S2, S3 etc. are not established with certainty. Shergold remarked that the glabellar furrows of *C. vietus*, which are weak, cannot be distinguished from faint muscle scars on the glabellar lobes (Shergold 1980, pl. 34, fig. 3). Furrows are present in a corresponding position in *C. discoidalis*, and an interpretation is given in text-fig. 3. Similar structure is also visible in the holotype of *Sayramaspis tenacella* Xiang and Zhang, 1985 and this may also be referable to *Cermatops*, though the pygidium (at present unknown) is needed to provide confirmation. The form of the S1 furrows and the presence of a median glabellar node in *C. discoidalis* indicate that it is not closely related to the Dikelocephalidae, in which S1 is commonly transcurrent and there is no preoccipital node.

Pygidial structure. The pleural regions of the pygidium are well segmented but behind the anterior segment the propleural band (the anterior part of an individual segment) is reduced, both longitudinally and transversely (Pl. 2, fig. 2). This is seen also in *Tamdaspis* (Ergaliev 1980, pl. 19, fig. 8) and, less distinctly, in *Guozia* (Xiang and Zhang 1985). Both these genera differ from *Cermatops* in their glabellar form.

A similar pygidial structure was independently derived in the Dikelocephalidae, for example *Briscoia septentrionalis* Kobayashi, 1935*a* (Palmer 1968, pl. 15, figs. 3 and 4). Pygidia of remarkably similar form have also been described in the family Aphelaspidinae under the generic names *Duibianaspis* Lu and Lin (1984, pl. 7, figs. 8, 9, 12, 13) and *Pseudaphelaspis* (*Arrhenaspis*) Qian (1985, pl. 6, figs. 4–7). (Note that the name of the type species of the latter genus, *P.* (*A.*) *latelimbata* Qian, 1985, is unavailable, being a primary junior homonym of *Pseudaphelaspis latelimbata* Lu and Lin, 1984.) In each of these genera the pygidium was associated with a typical aphelaspidid cranidium, and if they are correctly so assigned the genera are synonymous. However, those authors have not considered the possibility that the pygidia belong to *Cermatops* or *Tamdaspis*. Compared with the pygidia of *Cermatops*, that attributed to *Duibianaspis typicalis* Lu and Lin, 1984 has a blunt axis that is barely half the pygidial length, and that attributed to *P.* (*A.*) '*latelimbata*' Qian, 1985 is proportionally much wider, and recalls *Tamdaspis*.

The pygidium from the *Elvinia* Zone in a borehole in Montana, figured by Lochman (1964, pl. 11, fig. 7) as *Pterocephalia sanctisbae* Roemer, differs from other figured pygidia of that species but bears a great likeness to *C. discoidalis*, though it differs in having the ventral terrace ridges half as densely spaced. The generic assignment of this pygidium is uncertain because none of the associated cranidium is likely congeneric with it.

Family relationships. Cermatops is regarded as a member of the Iwayaspidinae (Shergold 1980). This group shares several characters, for example the form of the glabellar furrows, the presence of a median preoccipital tubercle and a median suture, with primitive Asaphidae (in the sense of Fortey and Chatterton 1988) and the Ceratopygidae, but it lacks any convincing autapomorphy; it is a paraphyletic group, and we find the usual difficulties in assessing the relationships of the taxa within such a group.

The genera referred to the Iwayaspidinae commonly have a narrow cephalic border (compared with typical Asaphidae), a distinct preglabellar field and genal spines that are narrower at their base than the width of the cephalic doublure; the thorax varies, with 8–10 segments. These features are not seen in the Asaphidae but are met with in the Ceratopygidae. Therefore we agree with Shergold (1980, p. 86) and Fortey and Chatterton (1988, p. 196) that the Iwayaspidinae are better referred to the Ceratopygidae than the Asaphidae.

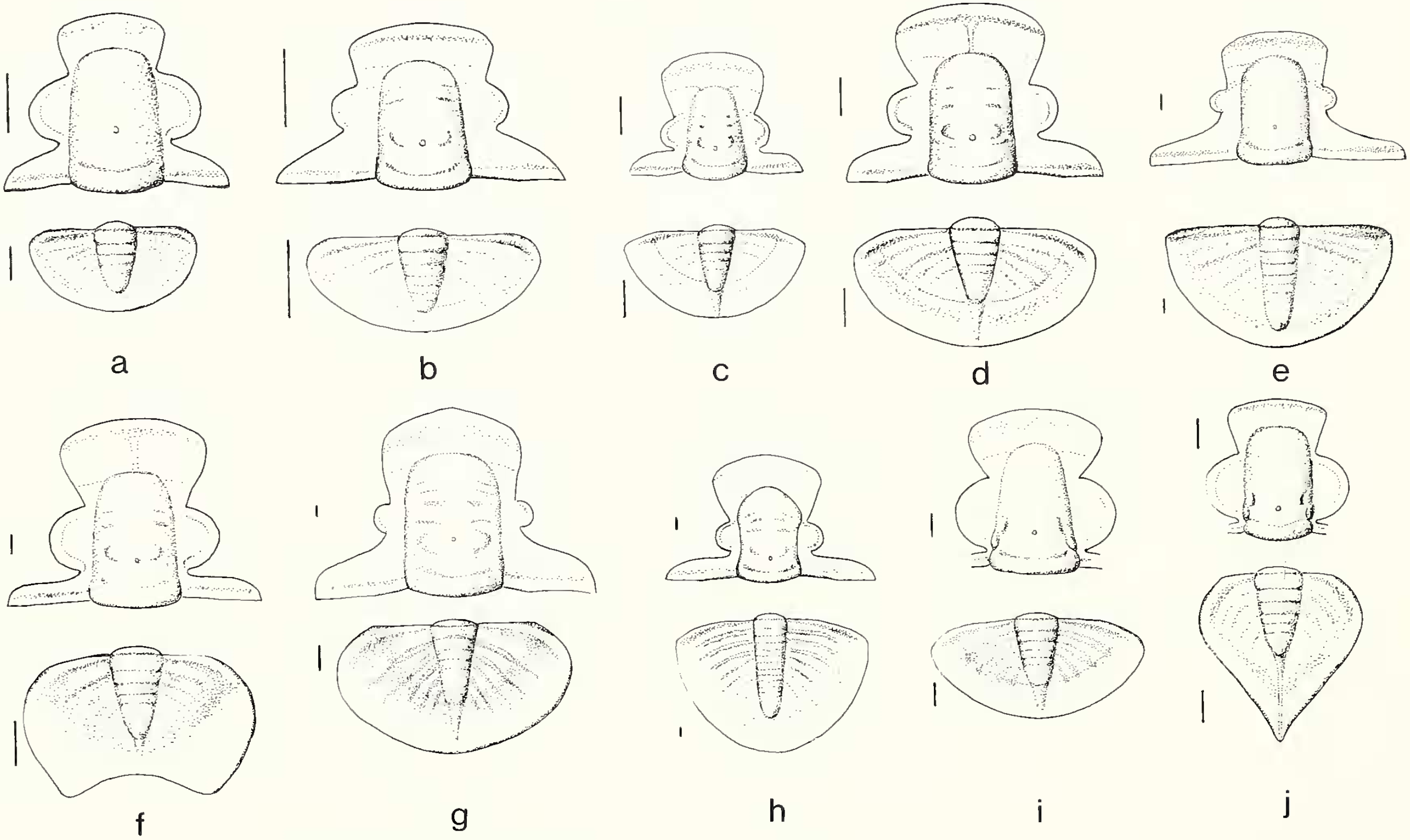
The typical Ceratopygidae (Subfamily Ceratopygidae) are characterized especially by the presence of marginal spines in the pygidium that are derived from macropleural segments. The capacity to develop such spines is taken as an autapomorphy for the subfamily, although it is evident that not all such spines are homologous (for example they are developed from the tenth post-cephalic segment in *Proceratopyge* but the eighth in *Dichelepyge*). Fortey and Chatterton (1988) justifiably referred the Macropyginae to the Ceratopygidae; this subfamily is characterized by baccular lobes on the cephalon and an exceptionally elongate pygidium (text-fig. 5*i*, *j*).

Several genera have been referred to the Iwayaspidinae, as follows: the type genus *Iwayaspis* Kobayashi, 1962 (type species *I. asaphoides* Kobayashi) has been regarded as a junior synonym of *Pseudoyuepingia* Chien, 1961 (type species *P. modesta* Chien), e.g. by Jago 1987. Other genera are *Yuepingia* Lu, 1956 (type species *Y. niobiformis* Lu), *Aplotaspis* Henderson, 1976 (*Charchagia erugata* Whitehouse, 1939), *Cermatops* Shergold, 1980, *Guozia* Xiang and Zhang, 1985 (*G. crassa* Xiang and Zhang) and *Sayramaspis* Xiang and Zhang, 1985 (*S. angustaxis* Xiang and Zhang). *Haniwoides* Kobayashi, 1935*b*, based on *H. longus* Kobayashi, is imperfectly known but is probably an iwayaspidine; it generally resembles *Yuepingia* apart from the apparent absence of a median glabellar tubercle. *Haniwoides*? *varius* Shergold, 1980 (and probably also *H.*? *puteolatus* Kobayashi, 1962), though doubtfully referred to the genus, has all the features of an iwayaspidine. *Norinia* Troedsson, 1937 has the typical arrangement of glabellar furrows but has a relatively short, undifferentiated preglabellar field, and it may be better referred to the Asaphidae. *Charchaqia* Troedsson, 1937 has the axial features effaced and is therefore difficult to evaluate, as already noted by Troedsson.

Tamdaspis Lisogor, 1977 can be interpreted as an advanced Iwayaspidine but, depending on how its special features such as the bacculae are evaluated, it may be regarded as a primitive member of the Macropyginae (text-fig. 5*i* and *j*). *Psiloyuepingia* Qian and Qiu, 1983 (in Qiu *et al.* 1983) is doubtless a synonym of *Tamdaspis*. We exclude *Pseudohysterolenus* Harrington and Leanza, 1957 because it differs from all iwayaspidine genera in the posterior position of the glabellar node. We also exclude *Metayuepingia* Liu (in Zhou *et al.* 1977), *Yuepingioides* Lu and Lin, 1984 and *Parayuepingia* Zhou *et al.*, 1982) from the Iwayaspidinae. All have short frontal areas, little or no preglabellar fields, and in the first two forms the genal angle is rounded.

Most of the above taxa have been proposed since publication of the Treatise Volume O (Moore 1959), and examples are illustrated here in text-fig. 5. Although many of their features are primitive with respect to the Asaphacea a few characters may be regarded as advanced when considering relationships within the group:

1. Reduction of the interocular cheeks. Early *Proceratopyge* and Asaphidae have the palpebral lobe separated from the glabella by a distance about equal to the length (sag.) of the occipital ring, and this is taken to be the primitive condition. In several species of Iwayaspidines and Ceratopygines the palpebral lobe is enlarged and approaches the glabella. As the anterior end of the palpebral lobe in all such forms lies near S3 and L4, those forms with a longer palpebral lobe necessarily have a more transverse postocular suture (Jago 1987, p. 227).
2. The development of baccular lobes in the adult (as in *Tamdaspis*, text-fig. 5*i*).
3. The reduction of the propleural band in the pygidium (e.g. *Cermatops*, text-fig. 5*g*).
4. The development of a large posterior indentation in the pygidium (as in *Haniwoides*? *varius*, text-fig. 5*f*).
5. Effacement (e.g. in *Yuepingia*) is also regarded as a progressive feature but is so general as to be without classificatory value.
6. The presence of an auxiliary pair of glabellar furrows intercalated between SO and S1 appears to be a specialized character but its distribution is sporadic. It is present in *Cermatops discoidalis* and in single species of *Guozia* (*G.*? *dubia*), *Yuepingia*? ('*Iwayaspis*' *caelata*, text-fig. 5*d*) and



TEXT-FIG. 5. Examples of Iwayaspidinae. *a. Yuepingia niobiformis*, after Lu 1956, pl. 1, figs. 6 and 8. *b. Pseudoyuepingia modesta*, after Chien 1961, pl. 3, fig. 5. *c. Aplotaspis erugata* (Whitehouse), after Henderson 1976, mainly pl. 48, fig. 17, and pl. 49, figs. 1 and 2. *d.* '*Iwayaspis*' [= *Yuepingia*?] *caelata*, after Lazarenko, *in* Datsenko *et al.* 1968, pl. 16, figs. 6–10, drawn from photographs kindly supplied by Dr Lazarenko. *e. Sayramaspis yardanshanensis*, after Xiang and Zhang 1985, pl. 40, figs. 7–10. *f. Haniwoides*? *varius*, after Shergold 1980, pl. 32, fig. 8 and pl. 33, fig. 10, and Xiang and Zhang 1985, pl. 37, figs. 2–4. *g. Cermatops vietus*, after Shergold 1980, pl. 34. *h. Guozia crassa*, after Xiang and Zhang 1985, pl. 43, figs. 1–5, 7. *i. Tamdaspis tamdensis*, after Lisogor 1977, pl. 28 figs. 5–7, and Ergaliev 1980, pl. 18, fig. 17 and pl. 19, fig. 8. *j. Aksapyge foveata* Lisogor (Subfamily Macropyginae, for comparison with *Tamdaspis*), after Apollonov *et al.* 1984, pl. 2, figs. 9–14. Scale bars represent 2 mm.

TABLE 1. Coding of characters for selected taxa of the Iwayaspidinae. They are mostly the type species of their respective genera, but *Sayramaspis yardanshanensis* and *Pseudoyuepingia whitei* (Webby *et al.* 1988) were preferred on account of their good preservation. The pygidium of *Haniwoides convexus* was used, as that of *H. longus* is not known.

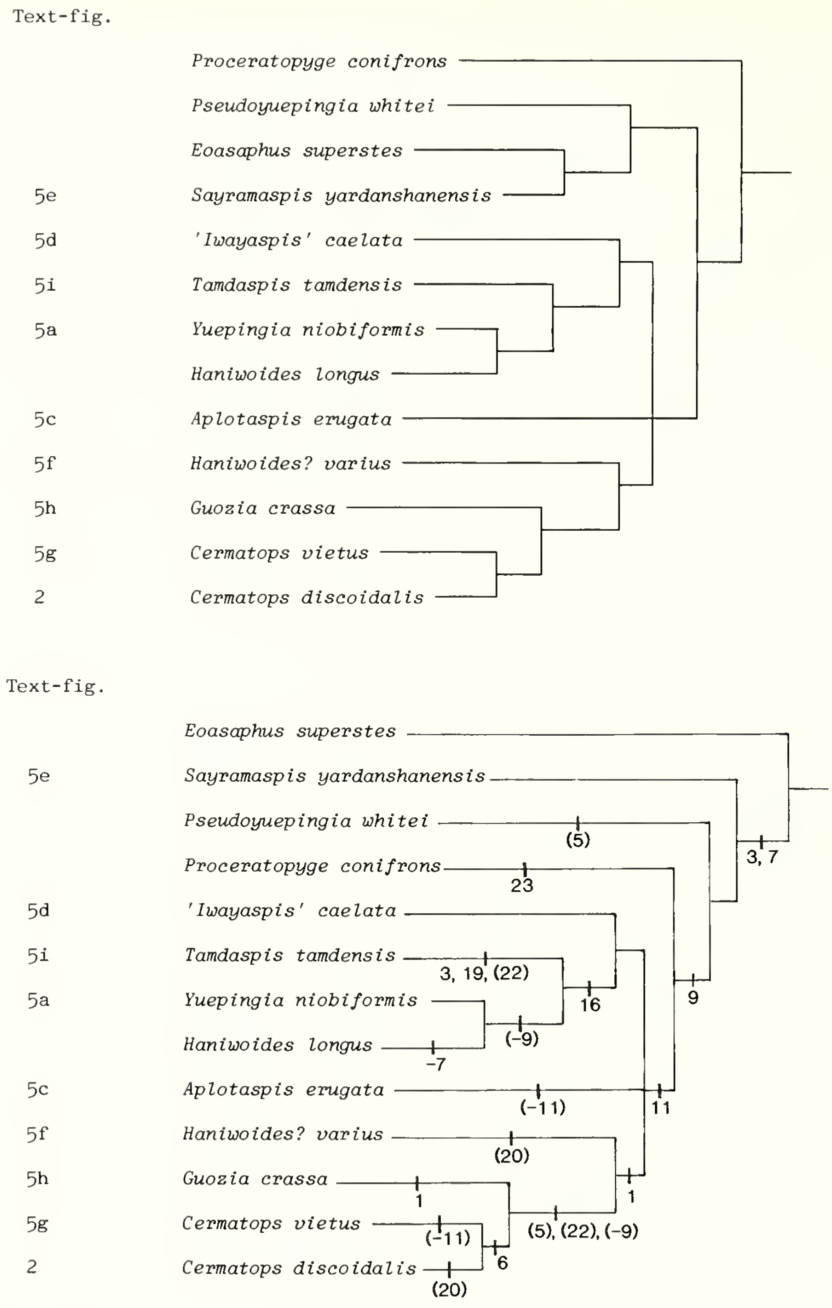
Character no.	1	2	3	4	5	6	7	8	9	10	11	12
Eoasaphus superstes	0	0	0	0	0	0	0	0	0	0	0	0
Proceratopyge conifrons	0	0	1	1	0	0	1	0	1	0	0	0
Sayramaspis yardanshanensis	0	0	2	0	0	0	1	1	0	0	0	1
Pseudoyuepingia whitei	0	0	1	0	1	0	1	0	0	0	0	9
'*Iwayaspis*' *caelata*	0	0	1	1	0	0	1	0	1	0	2	1
Yuepingia niobiformis	0	0	2	0	0	0	1	0	0	1	2	0
Aplotaspis erugata	0	0	1	0	0	0	1	1	1	1	1	1
Haniwoides longus	0	1	2	0	0	0	0	1	0	1	1	1
Tamdaspis tamdensis	0	0	3	0	0	0	1	0	1	1	2	1
Haniwoides? varius	1	1	1	0	0	0	1	1	1	0	2	1
Cermatops discoidalis	1	1	1	1	1	1	1	1	0	1	2	1
Cermatops vietus	1	0	1	0	1	1	1	1	0	1	0	1
Guozia crassa	2	1	1	1	1	0	1	1	0	0	2	1

Character no.	13	14	15	16	17	18	19	20	21	22	23
Eoasaphus superstes	0	1	1	1	1	1	0	0	1	0	0
Proceratopyge conifrons	0	0	1	0	0	0	0	0	0	0	1
Sayramaspis yardanshanensis	1	0	0	0	1	1	0	0	0	0	0
Pseudoyuepingia whitei	1	1	0	0	0	0	0	0	1	9	0
'*Iwayaspis*' *caelata*	1	0	9	1	2	0	0	0	1	0	0
Yuepingia niobiformis	0	0	9	2	2	2	0	0	0	0	0
Aplotaspis erugata	1	1	1	1	0	0	0	0	1	0	0
Haniwoides longus	9	0	0	2	2	2	0	0	1	0	0
Tamdaspis tamdensis	9	9	9	2	2	2	1	0	1	1	0
Haniwoides? varius	1	1	1	1	2	2	0	1	1	0	0
Cermatops discoidalis	1	1	1	1	2	0	0	1	1	1	0
Cermatops vietus	1	0	1	0	2	0	0	0	1	1	0
Guozia crassa	9	1	1	1	2	2	0	0	9	1	0

Characters 1–23, scored as follows.

1. Glabellar front: rounded 0, truncate 1, pointed
2. Glabellar sides: straight 0, concave 1.
3. Glabellar furrows: simple 0, asaphoid 1, effaced 2, only S1 developed 3.
4. Auxiliary furrow on L1: absent 0, present 1.
5. S4 furrow: absent 0, present 1.
6. Muscle-scars on glabella: absent 0, present 1.
7. Median glabellar tubercle: absent 0, present 1.
8. Occipital ring: simple 0, compound 1.
9. Plectral lines: absent 0, present 1.
10. Frontal area: border differentiated 0, not differentiated 1.
11. Preocular sutures: diverge at < 30° 0, 30°–60° 1, > 60° 2.
12. Paradoublural line on cranidium: absent 0, present 1.
13. Paradoublural line on free cheek: absent 0, present 1.
14. Length of genal spine: > half of rest of cheek 0, < half 1.
15. Width of genal spine at base: > width of doublure 0, < width of doublure 1.
16. Palpebral lobe length ÷ cephalic axial length: < 0·3 0, 0·3–0·4 1, < 0·4 2.
17. Distance of palpebral lobe from glabella: > length of occipital ring (SO) 0, = SO 1, < SO 2.
18. Ocular ridge: present 0, absent 1, palpebral lobe touches glabella 2.
19. Bacculae in adult: absent 0, present 1.
20. Pygidial margin: entire 0, emarginate 1.
21. Postaxial ridge: absent 0, present 1.
22. Pygidial pleurae: normal 0, propleurae reduced 1.
23. Pygidial marginal spines: absent 0, present 1.

(Score 9 where a character cannot be coded.)



TEXT-FIG. 6. Relationships of selected taxa in the Iwayaspidinae, as indicated by the PAUP program (see text). Top, consensus tree with *Proceratopyge conifrons* for out-group comparison. Below, alternative tree with a hypothetical ancestor for out-group comparison. *Eoasaphus* is the most primitive actual taxon analysed. Numbers refer to characters in Table 1; negative numbers indicate character reversals and numbers in parentheses indicate parallelisms.

Sayramaspis (*S. tenacella*, text-fig. 3*c*, possibly a species of *Cermatops*?). It is of uncertain value in classification.

7. The postaxial ridge is well developed in many Iwayaspidines but is absent in some genera (*Sayramaspis* and *Yuepingia*) and doubtfully present in others (*Pseudoyuepingia* and *Guozia*). The polarity of this feature is not clear.

To test the relationships of examples of the Iwayaspidinae twenty-three attributes of thirteen species were analysed using the PAUP (Phylogenetic Analysis Using Parsimony) program, as described by Fortey and Chatterton (1988). Table 1 shows the matrix of characters used. The type species of *Proceratopyge*, *P. conifrons* Wallerius (Westergård 1948), was included for out-group comparison because it is regarded as a primitive ceratopygine and is stratigraphically the earliest species.

When *Proceratopyge conifrons* was defined as the sister-taxon of the Iwayaspidinae, the program yielded two equally parsimonious but not very robust trees, differing only in the affiliation of *Aplotaspis*; the consensus tree is shown in text-fig. 6, top. An alternative analysis that compared the coded species with a hypothetical ancestor (which would score 0 in all columns of Table 1 – the Lundberg option) yielded a slightly different tree with the distal groupings unchanged but the basal dichotomies rearranged (text-fig. 6, below); this seems the more probable arrangement because it places *Eoasaphus*, which appears to lack the typical asaphine glabellar features, in the most primitive position. *P. conifrons*, which carries the autapomorphy of the Subfamily Ceratopyginae, branches off the tree above *Pseudoyuepingia*, in such a position that the Iwayaspidinae has to be regarded as a paraphyletic group. The results are viewed with caution because the attributes were mainly gleaned from descriptions and illustrations in the literature, and these are of uneven quality (a more reliable result could be obtained if the attributes were coded from actual specimens).

According to these analyses the Iwayaspidinae is a paraphyletic group of the Ceratopygidae that lacks the pygidial spines of the Ceratopyginae and the bacculae and median pygidial extension of the Macropyginae. The Iwayaspidinae fall into three groups: (1) primitive forms – *Eoasaphus*, *Pseudoyuepingia* and *Sayramaspis*; (2) a large-eyed group with *Haniwoides*, *Yuepingia* and *Tamdaspis*; (3) a more specialized group with *Cermatops*, *Guozia* and *H.*? *varius*. *Aplotaspis* appears as the sister taxon of (3) or of (2)+(3). We recognize that many of the features analyzed are not very compelling because several of them are known to have arisen independently in other groups. The most parsimonious of our cladograms includes several reversals of character-states: for example in *C. vietus* the small eyes and subparallel preocular sutures appear primitive in comparison with the rest of the taxa in its clade.

The analysis indicates that *Sayramaspis* is probably a synonym of *Pseudoyuepingia*, and *Yuepingia* of *Haniwoides*; these genera should be investigated further. If glabellar features are seen as most significant for classification *Tamdaspis* could be maintained as a distinct genus recognized by its bacculae (as well as its pygidial structure) and *Guozia* could likewise be separated from *Cermatops* by its distinctive glabellar shape.

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